



Impact of enhanced summer temperatures on the distribution and structure of zooplankton communities in the heated stratified lakes: Implications for climate change

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ABSTRACT

Long-term studies demonstrated that temperature increases of 3–6 °C above natural levels caused reduction in zooplankton biomass. We hypothesized that large-bodied species would respond more strongly to temperature increases than small-bodied species because they are less adapted to high temperatures. Studies were conducted in three similar stratified meso-eutrophic lakes with different thermal regimes. Enhanced temperature, migrations, food abundance and dissolved oxygen concentrations were analyzed as potential factors that could affect zooplankton biomass. The warmest lake differed from the other lakes by lower total biomass of zooplankton less abundance of large-bodied zooplankton species, smaller population body sizes of abundant cladoceran species and higher food concentrations. Day and night abundances of zooplankton did not differ between the vertical strata and between the pelagic and littoral zones in the three study lakes suggesting that zooplankton did not vertically or horizontally migrate. We suggest that decreases of dissolved oxygen below the epilimnion prevented zooplankton from vertically migrating. As a result, zooplankton accumulated in the epilimnion where temperatures were higher than in the lower strata. Regression analysis showed that temperature had a significant negative impact on the total biomass of zooplankton in the epilimnion of the warmest study lake. Therefore, our results are in accordance with the ecological Bergmann's and James' rules dealing with the temperature-size relationships.

1. Introduction

Temperature structures planktonic communities and distributions in stratified lakes (De Stasio et al., 1996; Helland et al., 2007; Meerhoff et al., 2007; Wagner and Adrian, 2011; Kratina et al., 2012; Shatwell et al., 2016). Climatic models predict that the surface temperature in European temperate lakes will rise by 2.3–5.3 °C and that the frequency and duration of summer heat waves will increase (IPCC, 2014). Lakes that are heated with discharged water from power stations can serve as model systems for predicting the consequences of enhanced temperature effects on plankton communities. Furthermore, planktonic communities have been able to exhibit relatively long-time adaptation to high temperatures in such heated lakes (Jeppesen et al., 2014).

Field and experimental results have demonstrated contradictory responses of planktonic communities to rising temperature. According to long-term studies, the biomass of zooplankton in the epilimnion of the Polish heated Lake Licheńskie was significantly lower than in the nearby colder Lake Ślesieńskie (Hillbricht-Ilkowska and Zdanowski, 1978; Tunowski, 1994, 2009a; Tunowski and Siergiejeva, 1998; Feniova et al., 2014). In contrast, phytoplankton abundance has been shown to increase at enhanced temperatures (George and Harris, 1985; Holzapfel and Vinebrooke, 2005). However, based on the studies performed in 81 European lakes located in different climate zones, climate affected zooplankton biomass mainly through top-down regulation by fish, but not directly by temperature (Gyllström et al., 2005). Analyses of data obtained from latitudinal and altitudinal gradients and cross-

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comparison studies showed declines in the biomass and density of zooplankton and, as a result, weakened grazing pressure of zooplankton on phytoplankton in warmer climates (Meerhoff et al., 2012).

Furthermore, experimental studies do not allow us to establish the mechanisms by which temperature affects plankton because in nature, temperature can interact with other factors that also influence zooplankton (e.g. with nutrient loading, fish pressure, dissolved oxygen concentration). For this reason, past experimental data has been rather contradictory. For example, some studies (Yvon-Durocher et al., 2010; Shurin et al., 2012) showed that temperature increases of 3.6°C resulted in decreases in phytoplankton abundance but did not affect zooplankton biomass in experimental mesocosms. However, similar incremental changes in temperature in another experiment caused decreases in crustacean biomass while phytoplankton biomass was not affected (Strecker et al., 2004). Thus, regardless of a large pool of experimental data of temperature effects on aquatic ecosystems, it is difficult to extrapolate these findings to natural waterbodies (Schindler, 1998).

We suggest that small- and large-bodied cladoceran species respond differently to increases in temperature. Small-bodied species have been shown to dominate at high (27°C) temperatures while large-bodied species dominate at low temperatures under experimental conditions (Feniova et al., 2011, 2013). The total biomass of cladocerans can also decrease at high temperatures due to shifts in the abundance of small-bodied species. In support, Moore and Folt (1993) suggested that temperature increases above 25°C favor the development of small-bodied species and can cause dramatic changes in the ecosystem structure of temperate lakes. Research on the long-term succession of sedimentary cladoceran assemblages showed a shift in abundance from large-bodied *Daphnia* to small-bodied species in alpine lakes in response to climate warming (Nevalainen et al., 2014). These findings are supported by the metabolic theory of ecology that suggests that large organisms retain more resources in their bodies because they flux energy more slowly through their metabolic pathways, and vice versa for small organisms (Brown et al., 2004).

Decreases in zooplankton biomass in the epilimnion of lakes during the daytime may potentially be related to diel vertical migration (DVM) to deep strata to avoid predation, ultraviolet (UV) radiation or to find optimal trophic and temperature conditions (Ringelberg, 2010; Wagner and Adrian, 2011; Williamson et al., 2011). Zooplankton can also distribute horizontally in lakes (De Stasio, 1993) through diel horizontal migrations (DHM, Burks et al., 2002). Therefore, while studying temperature effects on zooplankton biomass, it is necessary to determine how diel migrations affect daytime abundances.

Temperature increases can be accompanied by declines in dissolved oxygen concentrations (DO) below the epilimnion in stratified lakes (Adrian et al., 2009). It was found that due to oxygen shortage there may be a reduction of rotifer, cladoceran and copepod abundance (Roman et al., 1993; Pinel-Alloul et al., 2004; Galkovskaya and Mityanina, 2005). As a response to DO shortage in the lower strata, zooplankton may accumulate in the epilimnion where temperatures are higher causing indirect enhanced temperature effects on zooplankton. DO can also potentially regulate the spatial distribution of fish and their prey. For example, fish are less tolerant to low DO than *Daphnia* species (Larsson and Lampert, 2011). Therefore, areas with low DO that fish avoid can serve as refuges for cladocerans. However, there is also a DO threshold of approximately 1 mg L⁻¹ for *Daphnia* (Weider and Lampert, 1985), copepods (Roman et al., 1993) and rotifers (Elliott, 1973; Taggart, 1984). Low hypolimnetic DO concentrations (< 1 mg L⁻¹) prevented *Daphnia* from exhibiting diel vertical migration (Sakwińska and Dawidowicz, 2005). As such, crustaceans are not able to escape predators in the hypolimnion, their exposure to UV radiation increases and/or competitive interactions strengthen during the daytime (Williamson et al., 2011).

The goal of the present study was to recognize which factors were responsible for the species structure, size structure and biomass of

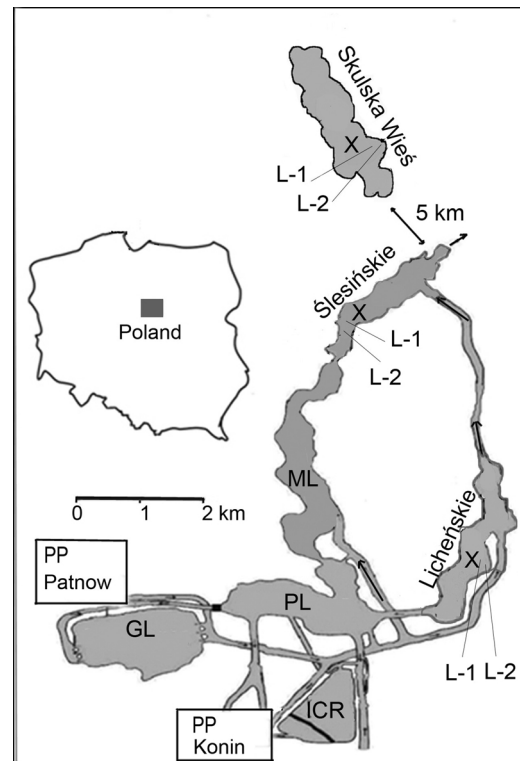


Fig. 1. Map of the Konin heated lake system. PP - Power Plant, ML - Mikorzyńskie Lake, PL - Pątnowskie Lake, GL - Gośławskie Lake, ICR - Initial cooling reservoir, X - stratified sampling stations, L-1 (depth 4–5 m) and L-2 (depth 2.5–3.0 m) littoral sampling stations.

zooplankton communities in three stratified Polish lakes with different thermal regimes. The potential regulating factors that we considered were enhanced temperature, vertical and horizontal migrations, algal food abundance and DO. We hypothesized that zooplankton biomass would decline at increased temperature due to: first, a shift in the abundance of large-bodied to small-bodied species in accordance with Bergmann's rule (Bergmann, 1847); second, due to a decrease in mean body size at the population scale (Daufresne et al., 2009) of zooplankton taxa in conformity with James' rule (James, 1970). We also anticipated that phytoplankton abundance would increase with rising temperatures as a result of direct temperature effect as well as due to reductions in zooplankton grazing pressure on phytoplankton.

2. Materials and methods

2.1. Study sites

The study was conducted in three meso-eutrophic Polish lakes with varying thermal regimes in 2011 (Fig. 1). The warmest was Lake Licheńskie (LI, 52°19.3'N, 18°20.6'E) which receives heated discharged water all year round. Lake Ślesieńskie (ŚL, 52° 23.4'N, 18°19.9'E) is heated from May to September (Staweski et al., 2007). Lake Skulska Wieś (SW, 52°28.3'N, 18°20.6'E) is located 5 km away from the heated lakes and was considered as a control. The lakes were similar in their morphometric and hydrochemical characteristics (Table 1, Hillbricht-Ilkowska and Zdanowski, 1978; Pyka et al., 2007).

2.2. Temperature and dissolved oxygen concentration (DO)

DO and temperature were measured from the surface to the bottom at 1 m interval with a YSI 5740 Dissolved Oxygen and Temperature Probe (Yellow Springs Instruments Co, Inc., Yellow Springs, Ohio, USA). The upper boundaries of epilimnion, metalimnion and

Table 1
General characteristics of the three study lakes.

	Licheńskie	Ślesieńskie	Skulska Wieś
Area (ha)	153.6	148.1	124.3
Max. depth (m)	13.3	25.7	17.5
Mean depth (m)	4.9	7.5	6.5
Retention time (day) ^a	3–5	7–9	14–30
Mictic type	monomictic	dymictic	dymictic
Trophic type	meso-eutrophic	meso-eutrophic	meso-eutrophic
Mean N_{tot} content (mg L^{-1}) ^b	1.3	1.3	3.5
Mean P_{tot} content (mg L^{-1}) ^b	0.089	0.099	0.06 ^c
Secchi depth (m)	1.77–2.13	1.9–2.37	1.65–2.03

^a data after Staweski et al., 2007.

^b data after Pyka et al., 2007.

^c data after Raport, 2006.

hypolimnion strata were determined based on the temperature profiles. Water transparency was measured with a Secchi disk.

2.3. Sample collection

Samples of cladocerans and copepods were collected from the epilimnion, metalimnion and hypolimnion strata with closing plankton net at noon and at midnight in the deepest site of each lake (Fig. 1). We took samples at noon and midnight on two dates in July and two dates in August 2011. The samples were immediately fixed with 4% formaldehyde. All cladocerans and adult copepods were identified to species. Immature stages of all copepod species were cited as juveniles. At least 30 in. of rare crustacean species and 100 in. of abundant species were measured to estimate biomass (wet weight) using length-weight relationships (Balushkina and Winberg, 1979).

The abundant cladoceran species individuals were divided into size classes with a length range of 0.025 mm each. Biomasses of each species and size classes of the abundant cladoceran species were estimated using length-weight relationships (Balushkina and Winberg, 1979). Crustacean species that contributed less than 5% of the total biomass were combined in the group “others”. Fecundity (mean clutch size per egg-bearing female) was calculated for every dominant cladoceran species in every stratum of each study lake. Additionally, cladoceran samples were collected during the second sampling date at sites with depths 4–5 m (L-1) and 2.5–3 m (L-2) to determine horizontal distribution of zooplankton (Fig. 1).

Rotifers were collected with a semiautomatic 5 L Toñ sampler (identical to the Ruttner sampler) at 1 m intervals. Rotifer samples were combined for each strata and fixed with Utermöhl solution (Utermöhl, 1958). At least 100 individual rotifers were counted with a calibrated ocular micrometer (Nikon Eclipse-E600, Nikon, Tokyo, Japan) to the nearest μm , excluding appendages in each sample and identified to species. Biomass was estimated using length-weight relationships (Ejsmont-Karabin, 1998).

Samples for chlorophyll concentration were collected in the epilimnion, metalimnion and hypolimnion using a Toñ sampler at 1 m intervals. Chlorophyll concentration was measured with a PhytoPam fluorometer (Walz, Germany) that assesses total chlorophyll concentrations and the individual concentrations of green algae, brown algae (diatoms and dinophyta) and cyanobacteria. Cladocerans commonly consume food particles within the size range 1–35 μm (Geller and Müller, 1981). Therefore, we measured additionally chlorophyll of algae less than 35 μm that was collected after filtering lake water through a 35 μm mesh. On the first sampling date in July, phytoplankton samples of 0.5 L were taken for microscopic analysis in each strata of the three study lakes. The samples were fixed with formaldehyde (4% solution). Algae were identified to genus or species.

Phytoplankton species biovolume was determined by associating the algae with similar geometric forms and used the standardized equations resulting of several shape measurements (Hillebrand et al., 1999).

2.4. Statistical analyses

Since maximum depths were different in the study lakes, we compared the investigated parameters (DO concentration, temperature, chlorophyll concentrations etc.) between identical strata along the vertical profile.

Decreases in zooplankton population densities at noon and increases at midnight in the epilimnion would suggest that zooplankton vertically migrate downward during the day and upward during the night. If there is no vertical migration, we expect that species abundances will be the same in the upper and lower strata at day and night. Repeated Measures Analysis of Variance (RM-ANOVA) was used followed by Tukey-HSD tests for multiple comparisons with equal variances according to the Levene criterion. Day time (the first two-level inter-group factor T: day, night), strata (the second three level inter-group factor L: epilimnion, metalimnion and hypolimnion) and sampling date (repeated measures: two or four level factor D: dates of sampling) were included in the RM-ANOVA to determine their effects on differences between day and night chlorophyll concentrations of cyanobacteria, green and brown algae and biomasses of individual zooplankton taxa contributing over 5% and “others” to the total biomasses of rotifers or copepods or cladocerans respectively. For rotifer vertical distribution, in SW only 2 dates were available. RM-ANOVA was also used to determine the differences between day and night horizontal distribution of cladoceran species contributing over 5% to the total zooplankton biomass and “others” in the deepest and littoral (L-1 and L-2) sites on different sampling dates. In this case, the three-level inter-group factor biotope (B: epilimnion, L-1, L-2) was used instead of strata-factor.

Since samples were collected on different dates in the three study lakes, one way-ANOVA was used to establish significant differences separately for temperature, phytoplankton, and zooplankton biomasses between the lakes. The data for different sampling dates from the same layers (at 1 m interval) for temperature and from the same stratified layers for phytoplankton groups (PAM data) and zooplankton taxa were used as replicates to determine whether there were differences between the three lakes in these parameters. Tukey’s HSD test was used to determine which treatments were significantly different ($P < 0.05$).

Multiple regression analysis was used to determine how temperature, DO and food abundance (concentrations of total chlorophyll and that of algae less than 35 μm) (independent variables) influenced total zooplankton biomass (dependent variables) in epilimnion of the three study lakes. Data were log transformed to meet the assumptions of normality of residuals.

Since the samples were collected on different dates in the lakes, we used Main Effect ANOVA to assess effects of two factors (Time and Lakes) on the biomass of small and large size classes of cladoceran species. We used Tukey’s Honestly Significant post-hoc test to establish significant differences. Species with individuals > 0.8 mm, i.e. over maximum size of small bodied species such as *Ceriodaphnia reticulata* (Jurine 1820), were referred to large bodied species. In order to verify Bergmann’s rule that says that the share of small-bodied species increases under warming, we found the ratio of biomass of small-bodied species of cladocerans to that of large-bodied species. Student’s *t*-test for independent variables was used to find significant differences between mean sizes of individuals among populations of cladocerans.

ANOVA analyses were carried out using Sigma Stat, version 4.0 (Systat Software).

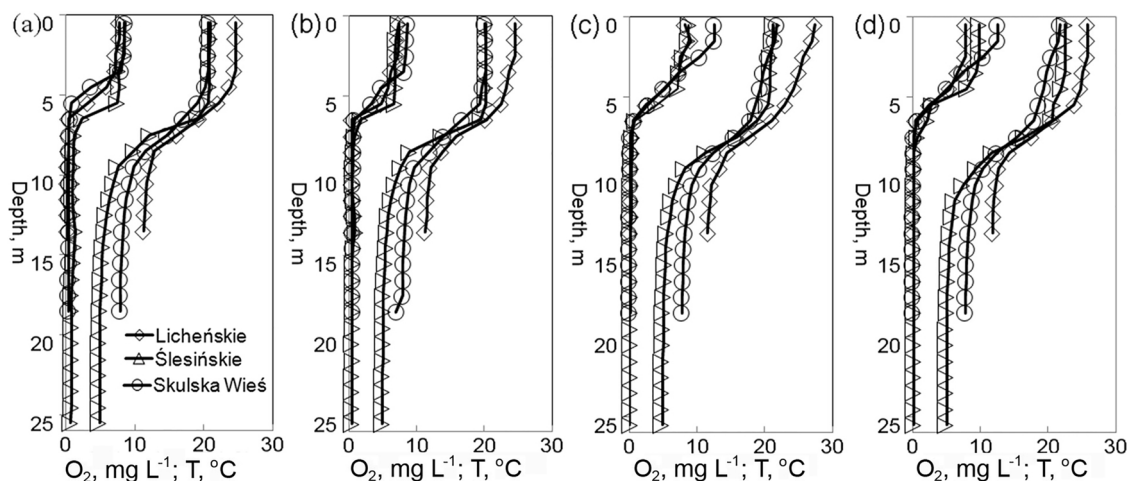


Fig. 2. Temperature (right profiles) and oxygen (left profiles) vertical profiles of the three study lakes (sampling date, a: 23–27 July; b: 29 July–2 August; c: 19–23 August; d: 25–29 August).

3. Results

3.1. Temperature and dissolved oxygen concentrations

In LI, temperature in the epilimnion and hypolimnion strata was higher than in the corresponding strata of the two other lakes (ANOVA, $P < 0.05$; Tukey's HSD, $P < 0.001$; Fig. 2, Table 2). In ŚL, temperature in the epilimnion was slightly (about 1 °C) higher (Tukey's HSD, $P < 0.005$) than temperature in SW. DO in the epilimnion was greater than 6 mg L⁻¹ in all the lakes. However, DO in the metalimnion abruptly declined below 1 mg L⁻¹ in all the lakes (Fig. 2, Table 2).

3.2. Phytoplankton vertical distribution in the three studied lakes

In SW and ŚL, chlorophyll concentrations in all the phytoplankton study groups (ANOVA, $P < 0.001$; Tukey's HSD, $P = 0.901$) and that of edible fraction (ANOVA, $P < 0.001$; Tukey's HSD, $P = 0.972$) were similar (Fig. 3). In LI, chlorophyll concentrations of the phytoplankton groups were significantly higher than in the other two lakes (ANOVA, $P < 0.001$; Tukey's HSD, $P < 0.001$). In all of the lakes, chlorophyll concentration of edible phytoplankton fractions constituted 85–91% of the total chlorophyll concentration. In SW and ŚL, chlorophyll concentration did not differ significantly along the vertical profiles (Fig. 3). However, in LI, distributions of the chlorophyll concentrations were different. There was a pronounced peak of chlorophyll concentrations (ANOVA, $P < 0.001$; Tukey's HSD, $P < 0.001$) in the metalimnion while in the other two lakes, chlorophyll concentration gradually declined downward. Diatoms were distributed evenly in SW and ŚL while

in LI they accumulated mostly in the metalimnion. In LI, diatoms were the most abundant group in the lower strata, while cyanobacteria and green algae were extremely rare. In SW and ŚL, cyanobacteria and green algae were present in all of the strata, yet, their abundance decreased with depth. We found a weak negative correlation of the water transparency with the total chlorophyll concentration ($r = -0.21$, $p > 0.05$).

Chlorophyll concentrations of the phytoplankton groups did not vary significantly between day and night hours in the epilimnion, metalimnion and hypolimnion (RM-ANOVA, Table 3). Nevertheless, chlorophyll concentrations varied significantly between the sampling dates and between strata, besides, their interaction effects were also significant (Table 3).

Phytoplankton abundance data derived from microscopic analysis were in accordance to chlorophyll concentration distribution. There were also no significant differences found between day and night values. In ŚL and SW, the most abundant algae were Dinophyta and Chlorophyta. In SW, cyanobacteria were present. Diatoms were commonly abundant in the metalimnion.

In LI, Dinophyta (*Peridinium borgei* (Lemmermann 1910) contributed > 30% to the total biomass, diatoms (*Stephanodiscus* sp.), Cryptophyta (*Cryptomonas ovate* (Ehrenberg 1832)) dominated in epilimnion and metalimnion, and green algae (*Crucigenia tetrapedia* (Kuntze 1898), *Scenedesmus quadricauda* (Turpin) Brébisson 1835) were mostly abundant in the hypolimnion. In ŚL, Dinophyta (*Peridinium borgei* (Lemmermann 1910)) constituted > 60% of the total biomass in the epilimnion. The same species of green algae as in LI together with *Phacotus* sp. and *Cosmarium reniforme* ((Ralfs) W. Archer 1874) were abundant in ŚL. Although SW is not connected to the heated lakes, the edible fraction consisted of the same phytoplankton species. *P. borgei* accounted for 45–50% of the total biomass and the green alga *C. tetrapedia* made up to 30% in the upper layers of this lake.

3.3. Zooplankton vertical distribution in the three studied lakes

The biomass of rotifers, cladocerans and copepods was the highest in the epilimnion of LI and SW (Fig. 4). In ŚL, *Asplanchna* sp. was abundant on the one of the sampling dates in the metalimnion which resulted in a higher mean biomass of rotifers in this strata at night. In LI, the biomass of *Daphnia cucullata* (G. O. Sars 1862) was similar in the epilimnion and metalimnion. However, the percentage of *D. cucullata* in the total cladoceran biomass was only about 3–10% in epilimnion. There was no significant difference between the biomass of zooplankton species at noon and at night; however, strata and the strata * date interaction had significant effects on species biomass (RM-ANOVA,

Table 2

Mean and minimal (min)-maximal (max) temperatures and dissolved oxygen concentrations during the study period (two dates in July, two dates in August) in the different stratified layers of the three study lakes.

Lake	Stratum	Temperature (°C)		Oxygen (mg L ⁻¹)	
		mean ± SD	max-min	mean ± SD	max-min
Licheńskie	epi-	24.5 ± 1.6	27.4-19.4	6.5 ± 1.8	9.1-2.4
	meta-	17.4 ± 3.1	22.2-12.7	0.6 ± 0.8	3.2-0.2
	hypo-	11.9 ± 0.5	13.4-11.3	0.3 ± 0.1	0.4-0.1
Ślesieńskie	epi-	20.9 ± 1.0	22.6-18.9	7.8 ± 1.3	9.8-4.0
	meta-	10.1 ± 3.2	16.6-6.8	0.7 ± 0.5	2.1-0.1
	hypo-	5.2 ± 0.4	6.4-4.9	0.4 ± 0.4	1.4-0.1
Skulska Wieś	epi-	20.1 ± 1.0	21.8-17.9	7.0 ± 3.6	12.6-2.8
	meta-	12.4 ± 2.7	17.0-9.3	0.4 ± 0.2	0.8-0.2
	hypo-	8.2 ± 0.4	9.0-7.0	0.3 ± 0.2	0.5-0.1

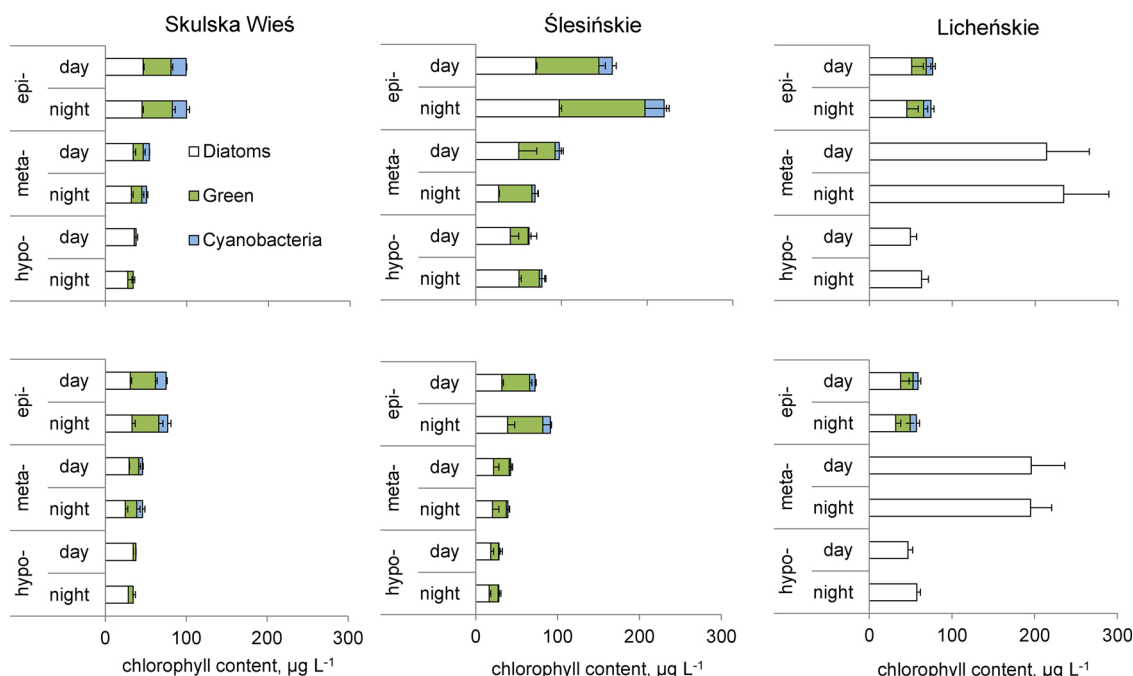


Fig. 3. Day and night chlorophyll concentrations (PHYTO-PAM fluorometer data) of three algae groups (on the top) and that of algae under 35 µm (on the bottom) in epi-, meta-, hypolimnion of the three study lakes. The vertical bars represent the standard deviation.

Table 3).

In the epilimnion of LI, the total rotifer biomass was lower than in ŚL (ANOVA, $P < 0.001$; Tukey's HSD, $P < 0.001$). Differences in rotifer biomass between ŚL and SW were not significant (Tukey's HSD, $P = 0.228$). In LI, the rotifer community was mostly represented by

small-bodied species (Fig. 4). In ŚL, small-bodied and large-bodied (*Asplanchna* spp.) species were equally abundant. In SW, *A. priodonta* (Gosse 1850) contributed the greatest share to total rotifer biomass.

In LI, the total cladoceran biomass in the whole water column and in the epilimnion was significantly less than in the corresponding layers in

Table 3

Results of RM-ANOVA of influence of sample dates (D, repeated measures: two or four level factor), stratified layers (L, three level inter-group factor: epi-, meta-, hypolimnion) and day/night (T, two-level inter-group factor) on biomasses in different phytoplankton taxa, rotifers and cladocerans (for each species with biomasses over 5% of the total biomass and "others"), copepods (biomasses of adults and juveniles) in the three study lakes.

Dependent variables	Lake	Licheńskie				Ślesieńskie				Skulska Wieś			
		Source of variation	df	MS	F	P	df	MS	F	P	df	MS	F
Phytoplankton (PHYTO-PAM data)	T	1	347.727	0.0	0.887	1	372.039	0.5	0.497	1	21.798	0.0	0.882
	D	1	8856.877	11.3	0.004	1	37.796	1.9	0.192	1	89.872	51.6	0.000
	D*T	1	0.326	0.0	0.984	1	109.103	5.4	0.034	1	42.213	24.2	0.000
	L	2	33774.777	6.2	0.005	2	4313.671	40.9	0.000	2	4290.013	112.9	0.000
	L*T	2	134.921	0.0	0.976	2	83.934	0.8	0.460	2	9.290	0.2	0.785
	L*D	2	2085.529	6.5	0.004	2	257.558	10.9	0.000	2	3.076	0.3	0.732
	L*D*T	2	1.005	0.0	0.997	2	174.018	7.4	0.002	2	9.916	1.0	0.374
Rotifers	T	1	0.00002	0.0	0.915	1	0.00196	0.77	0.405	1	0.00288	0.5	0.505
	D	3	0.00038	1.7	0.186	3	0.00143	0.97	0.423	1	0.03137	14.5	0.005
	D*T	3	0.00029	1.3	0.292	3	0.00142	0.97	0.424	1	0.00008	0.0	0.853
	L	2	0.01134	12.7	0.000	2	0.01575	7.61	0.005	2	0.02262	8.5	0.003
	L*T	2	0.00006	0.1	0.933	2	0.00601	2.90	0.084	2	0.00194	0.7	0.498
	L*D	6	0.00058	3.7	0.004	6	0.00129	1.01	0.427	2	0.00098	2.3	0.128
	L*D*T	6	0.00041	2.7	0.024	6	0.00130	1.02	0.422	2	0.00087	2.1	0.159
Copepods	T	1	0.029	0.0	0.953	1	0.567	0.0	0.885	1	3.476	0.5	0.561
	D	3	5.017	4.7	0.052	3	2.922	0.9	0.503	3	2.808	2.1	0.201
	D*T	3	0.882	0.8	0.527	3	2.600	0.8	0.546	3	2.417	1.8	0.245
	L	2	16.937	5.1	0.079	2	57.571	5.6	0.070	2	168.697	26.6	0.005
	L*T	2	0.006	0.0	0.998	2	2.248	0.2	0.813	2	5.053	0.8	0.512
	L*D	6	4.770	4.9	0.009	6	1.676	0.9	0.530	6	2.957	2.8	0.064
	L*D*T	6	0.394	0.4	0.861	6	1.961	1.0	0.445	6	1.795	1.7	0.212
Cladocerans	T	1	0.3448	0.63	0.458	1	1.1624	0.57	0.474	1	0.764	0.2	0.665
	D	3	0.0392	0.47	0.709	2	1.9489	7.69	0.005	3	0.686	1.7	0.191
	D*T	3	0.1483	1.77	0.189	2	0.0341	0.13	0.875	3	0.208	0.5	0.674
	L	2	2.5303	5.86	0.017	3	0.7022	4.87	0.009	2	23.832	11.1	0.001
	L*T	2	0.2068	0.48	0.631	3	0.2329	1.62	0.212	2	1.459	0.7	0.521
	L*D	6	0.0129	0.16	0.986	6	9.3131	16.97	0.000	6	0.311	1.0	0.425
	L*D*T	6	0.1393	1.73	0.142	6	0.2609	0.48	0.823	6	0.285	0.9	0.479

Df - degree of freedom; MS - mean square. P -values in bold indicate significant treatment effects at the 0.05 level ($P < 0.05$).

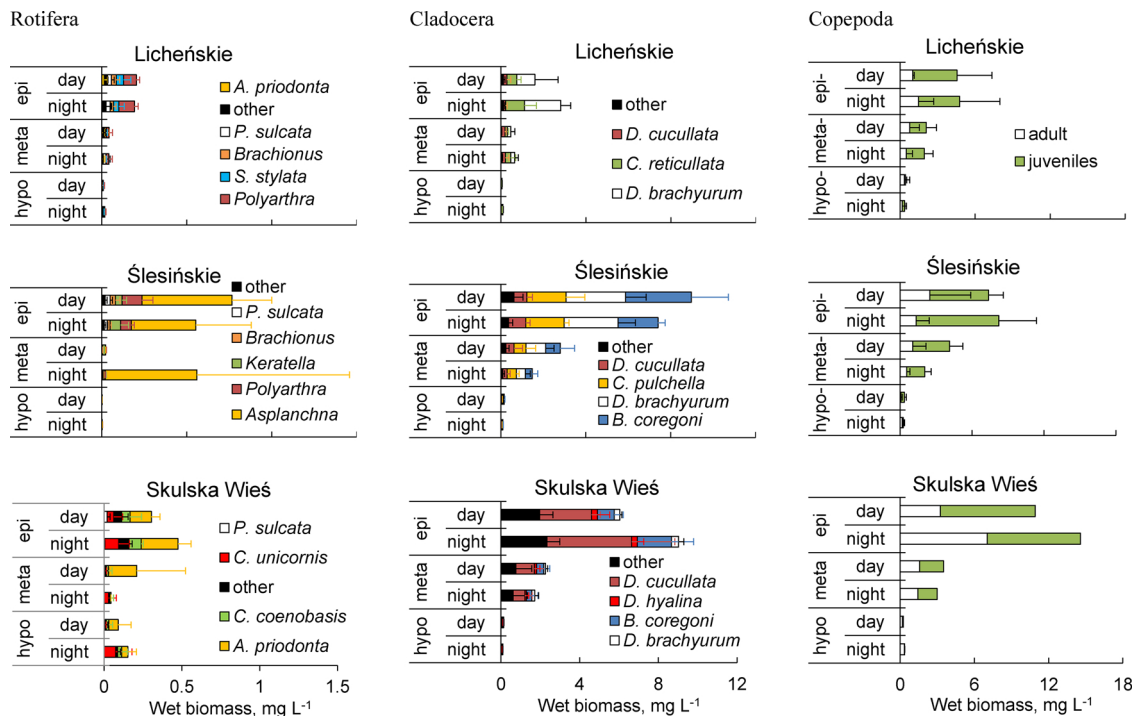


Fig. 4. Biomasses of rotifers, cladocerans (for each species over 5% of the total biomass and “others”) and copepods (biomasses of adults and juveniles) in the stratified layers of the three study lakes.

the other two lakes (Fig. 4). The differences in cladoceran biomass in the whole water column and in the epilimnion between ŚL and SW were not significant. In LI, only two species *Ceriodaphnia reticulata* (Jurine 1820) and *Diaphanosoma brachyurum* (Liévin 1848) were relatively abundant, while in the other two lakes species richness was higher. In the epilimnion, *Daphnia* abundance was the lowest in LI and it was the greatest in SW (ANOVA, $P < 0.001$; Tukey's HSD, $P < 0.001$) where *Daphnia* accounted for more than 50% of the total cladoceran biomass. Large-bodied species and *D. brachyurum* were rare in LI (ANOVA, $P < 0.000$; Tukey's HSD with ŚL, $P = 0.023$; SW, $P < 0.005$) while they were abundant in ŚL and SW.

The shallow biotopes of the three study lakes were inhabited by the same species as found in pelagic zone (Fig. 5). Total cladoceran biomass in the littoral was the lowest in LI (ANOVA, $P < 0.001$) as compared to the other two lakes (Tukey's HSD, $P < 0.05$). In the littoral, the biomass of *D. cucullata* was significantly lower in LI and ŚL than in SW (ANOVA, $P < 0.01$; Tukey's HSD, $P < 0.01$). No statistically significant differences in cladoceran biomass between day and night were found in the littoral of any of the three lakes. Only, time of sampling in SW ($F = 5.66$, $P = 0.039$, Table 4) significantly affected cladoceran biomass.

Total copepod biomass in the epilimnion (Fig. 4) was lower in LI and ŚL than it was in SW (ANOVA, $P < 0.01$; Tukey's HSD, $P < 0.02$). The biomass of adult copepods did not differ significantly between the heated lakes, LI and ŚL (ANOVA, $P < 0.005$; Tukey's HSD, $P < 0.799$), but it was lower than in SW (Tukey's HSD, $P < 0.02$). Juvenile (copepodite and nauplii stages) biomass in LI was lower than in SW (ANOVA, $P < 0.01$; Tukey's HSD, $P < 0.005$) but it was similar with that in ŚL (Tukey's HSD, $P = 0.131$), yet, it did not differ between ŚL and SW (Tukey's HSD, $P = 0.364$). In LI, the copepod community consisted of *Thermocyclops oitonoides* (G.O. Sars 1863), *T. crassus* (Fischer 1853) and *Mesocyclops leuckarti* (Claus 1857). In ŚL, the copepod community contained the same species found in LI and three additional species including the large-bodied *Eudiaptomus gracilis* (G.O. Sars 1862). In SW, all the above copepod species were found with *E. gracilis* being the most abundant. Additionally, the large-bodied *Eucyclops macrurus*

(G.O. Sars 1863) was found in SW whereas it did not occur in the other two lakes.

In LI, cladoceran eggs-bearing females were absent in the hypolimnion. In all the three study lakes, there were no statistically significant differences in cladoceran clutch sizes between their strata (Fig. 6) except *C. pulchella* in ŚL. Its fecundity in the metalimnion of this lake was lower than in the epilimnion and hypolimnion. Fecundity of *D. brachyurum* (ANOVA, $P < 0.05$; Tukey's HSD, $P < 0.05$) and *D. cucullata* (ANOVA, $P < 0.001$; Tukey's HSD, $P < 0.05$) were higher in LI than in ŚL and SW.

Multiple regression analysis showed that only temperature significantly negatively influenced the total zooplankton biomass in the epilimnion of the three study lakes (Table 5, Fig. 7). Regression models described the relationship between total zooplankton biomass with temperature, DO and phytoplankton abundance (adjusted $R^2 = 0.688$, $P = 0.006$).

3.4. Size classes of cladoceran species

Fig. 8 showed that in LI, the average size classes from 0.5 to 0.8 mm contributed more to the total biomass than the other size classes. In ŚL, the biomass of small size classes from 0.3 to 0.5 mm prevailed while in LI, intermediate size classes from 0.5 to 0.8 mm were more abundant. Large bodied species such as *D. longispina* and *D. hyalina* were abundant only in SW where the biomass of large classes over 0.8 mm were significantly higher than in the other two lakes (Fig. 9). The total biomass of individuals with sizes > 0.8 mm was larger in SW than in LI. The total biomass of individuals < 0.8 mm did not significantly differ between LI and SW but it was larger in ŚL than in SW (Fig. 9). The biomass ratio small-bodied: large-bodied species in cladoceran communities did not differ between LI and SW but it was higher in heated ŚL than in control SW. Means of body sizes were smaller in the heated lakes than in SW (Table 6).

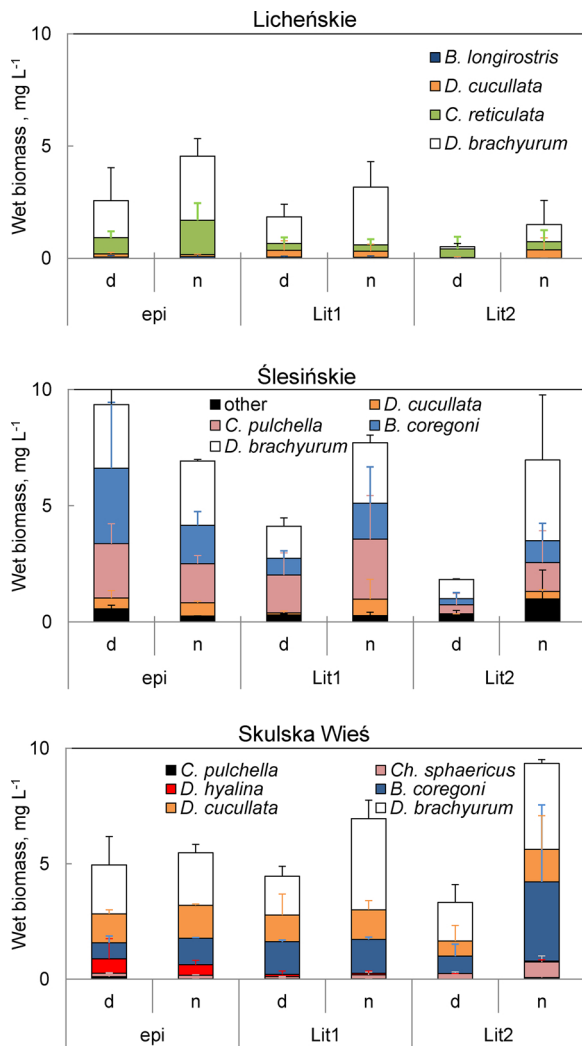


Fig. 5. Biomasses of cladoceran species of over 5% of the total biomass in epilimnion of deep and littoral (L-1, L-2 see Fig. 1) sites in the three study lakes.

4. Discussion

Day and night abundances of zooplankton did not differ between the vertical strata and between the pelagic and littoral zones in the three study lakes suggesting that zooplankton did not vertical or horizontal migrations. We found significant influence strata (L) and the strata * date (D) interaction on species biomass (Table 3). Since sampling was conducted in different dates in the lakes, factor D effects were assessed for the entire study period (more than a month). During such a long-term period, the abundance of any plankton taxa could change

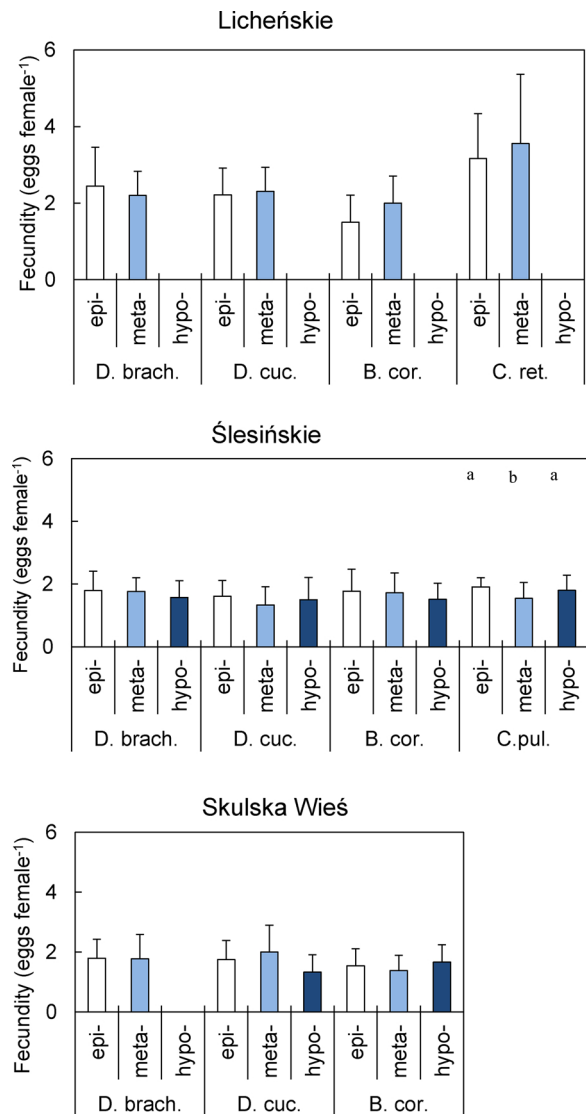


Fig. 6. Fecundity (clutch size) of cladoceran females (D. brach - *Diaphanosoma brachyurum*, D. cuc. - *Daphnia cucullata*, B. cor - *Bosmina coregoni*, C. ret - *Ceriodaphnia reticulata*, C. pul - *C. pulchella*) in the different stratified layers. The values that differed significantly (ANOVA, $P < 0.05$; Tukey's HSD, $P < 0.05$) are depicted by different letters.

strongly. As a result, the combined influence of the sampling date and stratum of the water column was statistically significant.

Rotifers and crustaceans were concentrated in the epilimnions of the three study lakes. Our study and previous ones (Hillbricht-Ilkowska and

Table 4

Results of RM-ANOVA of influence of sample dates (D, repeated measures: two level factor), biotops (B, three level inter-group factor, deep station epilimnion, littoral stations (L-1, L-2)) and day/night (T, inter-group factor) on biomasses in different cladoceran species (for each species with biomasses over 5% of the total biomass and "others") in the three study lakes.

Dependent variables	Lake	Licheńskie					Ślesieńskie				Skulska Wieś			
		Source of variation	df	MS	F	P	df	MS	F	P	df	MS	F	P
Cladocerans	T		1	0.612	0.7	0.427	1	1.080	0.2	0.645	1	4.546	0.7	0.419
	B		2	0.965	2.7	0.091	2	1.053	1.8	0.190	2	0.746	1.6	0.227
	B * T		2	0.537	1.5	0.246	2	0.716	1.2	0.315	2	0.930	2.0	0.163
	D		1	1.168	3.1	0.108	1	0.656	1.5	0.250	1	2.254	5.7	0.039
	D * T		1	0.017	0.0	0.837	1	1.829	4.1	0.066	1	0.092	0.2	0.641
	B * D		2	0.143	0.4	0.695	2	1.198	3.3	0.056	2	0.821	2.0	0.165
	B * T * D		2	0.105	0.3	0.764	2	0.936	2.6	0.099	2	0.995	2.4	0.117

Table 5
Results of multiple regression analysis of influence of temperature (T, °C), dissolved oxygen (DO, mg L⁻¹), food abundance (PHYTO-PAM, total chlorophyll concentration of algae under 35 μm) (independent variables) on the total zooplankton biomasses (B_{tot}, dependent variable) in the epilimnion of the three study lakes. Data were log transformed.

Independent variables	df	MS	F	P
Intercept	0.188	0.188	5.772	0.043
T	0.373	0.373	11.462	0.010
O ₂	0.013	0.013	0.391	0.549
PAM	0.005	0.005	0.148	0.710
Error	0.260	0.033		

Df - degree of freedom; MS - mean square. P-values in bold indicate significant treatment effects at the 0.05 level ($P < 0.05$).

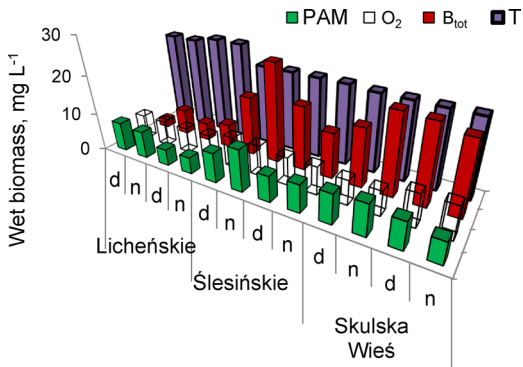


Fig. 7. Day (d) night (n) total biomasses (wet weight) of zooplankton (rotifers, copepods, cladocerans), temperatures (°C), oxygen concentrations (mg L⁻¹) and food abundance in terms of the chlorophyll concentration of algae under 35 μm in the epilimnions of the three study lakes.

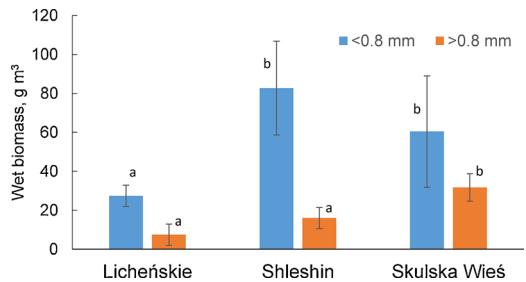


Fig. 9. Total biomasses (wet weight) of small-bodied (< 0.8 mm) and large-bodied (> 0.8 mm) cladoceran species in the three study lakes. Main Effect ANOVA (with factors: Sampling date and Lake) showed significant influence on the biomasses only of Lake factor ($p < 0.02$). Different letters represent differences between lakes. (Tukey's HSD, $p < 0.05$).

Zdanowski, 1978; Tunowski, 1994, 2009a; Tunowski and Siergiejeva, 1998; Feniova et al., 2014) showed that the biomass of all the studied zooplankton taxa, namely, rotifers, copepods and cladocerans, were the lowest in the warmest lake where epilimnion temperature exceeded 25 °C. Meerhoff et al. (2012) explained similar declines in zooplankton abundance in warm low latitude by increased fish predation. However, the reduced biomass of zooplankton in the present study was unlikely related to high fish predation. The planktivorous fish *Alburnus alburnus* (Vøllestad, 1985) occurring in the study lakes in high abundances constituted 39 and 62% of the total fish abundance in LI and ŚL respectively (Tereshchenko et al., 2007). Our previous study based on the contribution analysis by Polishchuk et al. (2012) showed that fish pressure was weaker in LI than in the other two lakes (Feniova et al., 2014).

Hence, we considered other potential factors that could have caused reductions in zooplankton biomass in the epilimnion of the warmest lake. One such factor could be diel vertical or horizontal migrations. Nevertheless, day and night biomasses of zooplankton species in the

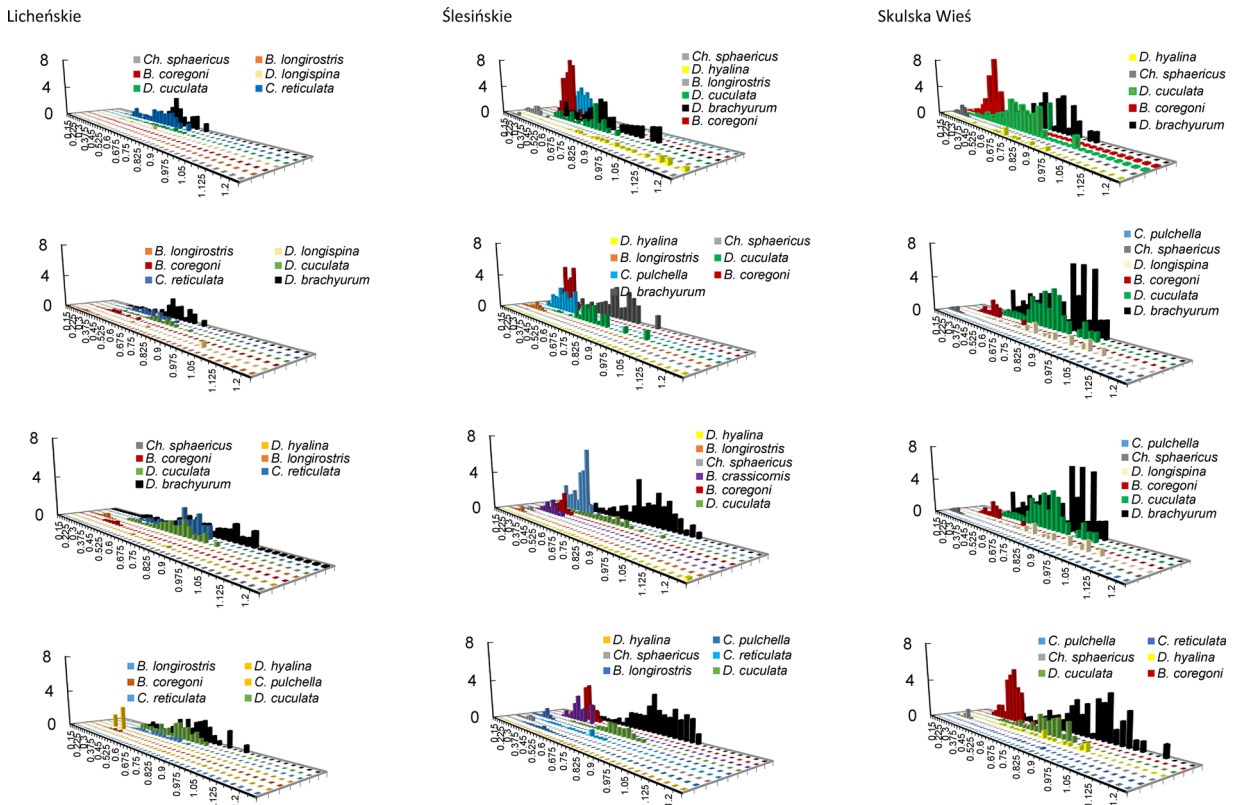


Fig. 8. Biomasses (wet weight) of different size classes of abundant cladoceran species in the three study lakes. Interval between size classes is 0.025 mm.

Table 6

The biomass ratio (mean \pm standard deviation (SD)) of small-bodied to large-bodied species in cladoceran communities, mean sizes (mm, mean \pm SD) of individuals in cladoceran populations of the study lakes. t – Student's t-values.

Lake	Licheńskie	Ślesieńskie	Skulska Wieś
mean proportion \pm SD	0.527 \pm 0.251	1.081 \pm 0.240	0.443 \pm 0.143
LI-SL	df = 6	t = 3.190	p = 0.019
LI-SW	df = 6	t = 0.580	p = 0.583
SL-SW	df = 6	t = 4.568	p = 0.004
<i>D.brachyurum</i>			
mean size \pm SD	0.619 \pm 0.153	0.624 \pm 0.154	0.687 \pm 0.169
LI-SL	df = 318	t = 0.302	p = 0.763
LI-SW	df = 318	t = 3.775	p = 0.000
SL-SW	df = 318	t = 3.479	p = 0.001
<i>D.cucullata</i>			
mean size \pm SD	0.576 \pm 0.132	0.586 \pm 0.117	0.653 \pm 0.147
LI-SL	df = 318	t = 0.703	p = 0.483
LI-SW	df = 318	t = 4.866	p = 0.000
SL-SW	df = 318	t = 4.449	p = 0.000
<i>B.coregoni</i>			
mean \pm SD		0.393 \pm 0.050	0.411 \pm 0.060
SL-SW	df = 318	t = 2.886	p = 0.004

stratified layers or pelagic and shallow biotopes did not significantly vary. Therefore, vertical and horizontal migrations did not occur in any of the three study lakes and could not affect species abundance in the epilimnion. Each zooplankton taxon commonly has a specific daytime vertical distribution. Large-bodied cladocerans prefer lower layers of water to avoid predation, ultraviolet radiation, etc. (Ringelberg, 2010; Williamson et al., 2011). However, they also concentrated in the epilimnion of the three study lakes. Rotifers were shown to frequently inhabit the epilimnion in hypertrophic lakes and metalimnion and hypolimnion in mesotrophic lakes (Galkovskaya and Mityanina, 2005). All the lakes in the present study were classified as meso-eutrophic (Carlson and Simpson, 1996) since their transparency was about 2 m in the summer. Thereby, rotifers should normally be located in the metalimnion. Copepods commonly locate in the metalimnion (Helland et al., 2007; Gladyshev et al., 2011) but in the three study lakes both copepods and rotifers were concentrated in the epilimnion.

Food abundance could have been another factor affecting zooplankton distributions in the three study lakes. The vertical distribution of edible phytoplankton ($< 35 \mu\text{m}$) was uniform with the exception of higher concentrations of phytoplankton in the metalimnion in LI (Fig. 3). The edible phytoplankton fraction in the three study lakes was mainly represented by species with high nutrient quality for zooplankton (Knisely and Geller, 1986; Ahlgren et al., 1990; Tessier et al., 2001; Ravet and Brett, 2006). Clutch sizes of cladocerans from various strata did not differ significantly indicating that there was no food limitation for zooplankton (Fig. 7). In the warmest lake LI, edible phytoplankton concentrations were greater than in the colder ŚL that was consistent with the greater fecundities of the abundant cladoceran species in this lake. Therefore, food resources did not appear to cause the reduction of biomass in LI.

We suggest that the uncommon distributions of zooplankton taxa, i.e. accumulation in the epilimnion, and absence of diel vertical and horizontal migrations in the three study lakes were caused by low dissolved oxygen concentration in the lower strata. In all the three study lakes, DO concentrations decreased sharply ($< 1 \text{ mg L}^{-1}$) below the epilimnion (Fig. 2, Table 2). Dissolved oxygen concentration was shown to be critical below 1 mg L^{-1} for rotifers (Elliott, 1973; Taggart, 1984), cladocerans (Weider and Lampert, 1985; Vanderploeg et al., 2009; Goto et al., 2012) and copepods (Roman et al., 1993). In general, DO deficiency in the hypolimnion of eutrophic lakes is a common phenomenon (Smith, 2003) and it can be strengthened by global warming (Ficke et al., 2007; Wilhelm and Adrian, 2008; Goto et al., 2012). According to recent studies, hypoxia occurred frequently in the lower strata of mesotrophic lakes due to the effects of climate warming

(North et al., 2014). In particular, in mesotrophic Lake Syta (Belarus), when epilimnion temperature increased up to 26.2°C , the DO concentration in the hypolimnion decreased below 4 mg L^{-1} and caused significant changes in the vertical distribution of zooplankton (Veznovets and Semenchenko, 2011). Therefore, hypoxia in the lower strata of the stratified lakes may be a greater structuring factor than previously thought. Specifically, we believe that hypoxia forced zooplankton taxa to accumulate in the epilimnion where they were subjected to temperature effects.

One more potential cause for small-bodied taxa domination in zooplankton and smaller zooplankton biomass in LI than in ŚL is a shorter water retention time in LI than in the other two lakes (Tunowski, 2009a). However, we conducted our studies in the period when LI and ŚL had almost identical water retention time (about 5 and 7 days, respectively). In accordance with data of 1999 (Tunowski, 2009a), total biomasses of zooplankton in ŚL in July decreased significantly compared to May and were close to those in LI in May. Cladocera constituted 80–90% of the total zooplankton biomass in LI and *D. cucullata* dominated in May. The nearly three-fold zooplankton biomass increase in LI was observed in the summer of 1996 when the temperature of water was lower by 4.4°C than it had been in the previous year (Tunowski, 2009a). Moreover, sampling sites in LI were outside the reach of the discharged water flow. The zooplankton biomass in the discharge canal from LI was the lowest than in the other canals of the heated lake system (Tunowski, 2009b). As such, the retention time must not have influenced the biomass of zooplankton. Thus, temperature regime is one of the main factors distinguishing study lakes and can be the main reason for the decline of abundance in *Daphnia* and other zooplankton taxa.

Regression analysis affirmed that temperature had a significant negative impact on the total biomass of zooplankton in the epilimnion of the three study lakes. We suggest that species of large-bodied zooplankton are more vulnerable to enhanced temperature than small-bodied species.

Data on biomass of individual size classes evidence in favor of this inference. In particular, in the warmest Lake LI, the total biomass of large bodied species with individual size over 0.8 mm was similar to that in the heated SL but it was much lower than in the non-heated SW. These data are in complete agreement with Bergmann's rule (Bergmann, 1847) which indicates that small-bodied species would prevail in warm environments. However, the biomass ratio of small-bodied to large-bodied species in the total biomass was similar in the heated LI and control SW. This can be related by high abundance of *Diaphanosoma*, which we consider as a large species, in all the studied lakes. This species frequently inhabits subtropical and tropical lakes (Atkinson, 1994; Pinto-Coelho et al., 2005). Meanwhile, the share of small-bodied species in the total biomass was significantly larger in the heated SL than in SW.

Moreover, in July 2010, maximum temperature in the epilimnion in LI was higher than in July 2011, and *Daphnia* species were absent during this period, yet, they appeared later after temperatures decreased (Feniova et al., 2014). Analysis of different groups of ectothermic aquatic organisms at both individual and community levels have shown that reductions in body is a general ecological response to global warming (Daufresne et al., 2009) that gives competitive advantage to small-bodied species (Reuman et al., 2014). Moreover, laboratory experiments with polycultures and monocultures showed that small-bodied cladocerans replaced the two larger *Daphnia* species at higher temperature, because their clearance rates increased faster than those of *Daphnia* at higher temperatures (Feniova et al., 2013). The total biomass of cladocerans was 2–5 times lower at 25°C than it was at 18°C (Feniova et al., 2011). All the above evidences strongly suggests that reductions in zooplankton biomass can be accompanied by decreases in the relative abundance and biomass of large-bodied zooplankton taxa.

5. Conclusions

We can predict that temperature increases above 25 °C under global climate warming may create shortage of dissolved oxygen in the lower strata that, in turn, strengthen the enhanced temperature effects on zooplankton species due to their accumulation in the epilimnion. Especially strong response to enhanced temperature is exhibited by large-bodied species resulting in the shift of species structure in favor of small species, decrease of population mean body size in accordance with Bergmann's and James' rules and reduction of the total zooplankton abundance.

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